FRONT COVER:
A group of trees killed by the Douglas-fir beetle in the Clearwater drainage.

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CHRONOLOGY AND CHARACTERISTICS OF A DOUGLAS-FIR BEETLE OUTBREAK IN NORTHERN IDAHO

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PREFACE

We hope that this account will provide technology and data for others who would seek to measure and describe future outbreaks of the Douglas-fir beetle in the Northern Rocky Mountains.

Our chronology began in 1971, two generations after beetles are thought to have bred to abundance in trees felled during clearing for Dworshak Reservoir. We entered the scene after standing trees were reported to be dying and continued the study until 1974 when the infestation waned. More recently, we have begun sampling infested and green stands, seeking to relate their characteristics to beetle susceptibility. Results of this work will be reported separately.

RESEARCH SUMMARY

A Douglas-fir beetle infestation that killed 111 million bd.ft. of sawtimber was studied over a 4-year period to determine factors associated with its occurrence and decline. Occurrence of the outbreak was associated with felled and damaged trees, dense stands of Douglas-fir, predominantly on good sites, and possibly root rots of which *Verticicladiella wagnerii* Kendrick was found in Douglas-fir for the first time. Tree mortality began declining during the third year of the infestation, accompanied by increased resistance of trees to attack; a beetle population index of 1.1 in the fall; and a higher proportion of immature overwintering brood. A verbal model is proposed to describe the functioning of factors that regulate beetle populations and damage. Preventive measures are suggested.

CONTENTS

INTRODUCTION

The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk., infests mainly Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, in which it periodically reaches epidemic levels (Furniss and Orr 1970). Historically, outbreaks in coastal areas have been attributed to catastrophic disturbances, especially windthrow. Relationships involving outbreaks in Rocky Mountain areas seem more diverse than elsewhere and have not been well documented and reported.

Study of Rocky Mountain infestations has been difficult due to lack of accurate, quantitative measurements of tree damage to which causal factors could be related. Detection of infested trees for damage measurement and population sampling is complicated by the time lag between beetle attack and reddening (fading) of foliage. Rate of fading varies considerably among trees and between years (Belluschi and Johnson 1968), probably influenced by attack density and moisture stress. Infested trees occur in groups, which contributes to variation between randomly distributed sample plots. Within individual trees, attacks are located so high that samples must be taken 10 ft or more above ground with a ladder or tree climbing device (Furniss 1962a).

Discovery of an outbreak in the Clearwater drainage of northern Idaho provided an opportunity to investigate factors involved with infestation trends. Biological studies were conducted with others who were seeking to develop and apply a photographic method to measure tree mortality (Ciesla and others 1971). The objective was to look for relationships among trend of tree mortality and factors involving insect populations and suceptibility of individual trees and stands. When understood, these relationships would be useful for predicting outbreaks.

BACKGROUND

In 1969 an outbreak of Douglas-fir beetles developed in the North Fork Clearwater River drainage. The beetles may have bred to epidemic levels in trees felled during clearing for Dworshak Reservoir and in snow-broken Douglas-fir surrounding the reservoir (Ciesla and others 1971). The previous Douglas-fir beetle outbreak in the Clearwater River drainage occurred in 1950-1952.[1] During those years, 7.6 percent of the merchantable Douglas-fir had been killed.

Severity of this most recent outbreak became evident in spring 1971 when foliage of infested trees turned red.[2] The damage occurred within approximately 270,000 acres of forest. Some infested trees were only 80 to 90 years old--much younger than we had encountered previously. Alarmed by this damage, members of the Northern Rockies Forest Pest Action Council undertook a cooperative survey of tree mortality by aerial photography and ground sampling to assist salvage logging operations.

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[1]Evenden, James C. Nov. 1952. Douglas-fir infestation, Northern Rocky Mountain Region. For. Insect Lab., Coeur d'Alene, Idaho, unpubl. rep., 9 p.

[2]Koppang, M. D. Clearwater-Potlatch Timber Protective Association, Orofino, Idaho, July 1, 1971, personal communication.

Although the outbreak had already been underway for 2 years, we decided to observe and sample the beetle population and associated factors until the infestation subsided; something never reported before in the Northern Rocky Mountains. This paper presents findings after observing four generations of beetles. We include information obtained in separate cooperative surveys of infested trees (Ciesla and others 1971; McGregor and others 1972; McGregor and others 1974).

METHODS

The area studied lies within the North Fork Clearwater River drainage between Elk Creek and the Little North Fork (fig. 1).

Trend of damage was determined from estimates of numbers and volumes of infested trees obtained from aerial photos and ground sampling. Beetle populations were measured on bark samples from infested trees. Other data were taken from individual infested trees and stands.

Damage

1971

The number and volume of infested trees on 288,000 acres were estimated by interpreting 100, 100-acre aerial photo plots and cruising 26 of these plots (Ciesla and others 1971). Plots were photographed in mid-August on a 9-inch format at a scale of 1:7,920 on Ektachrome infrared Aero (8443) film. The camera for this and subsequent photography was a Zeiss-RMKA 15-23 equipped with a 6-inch focal length lens and anti-vignetting color filter.

1972

The procedure was essentially the same as in 1971, except that 161, 100-acre photo plots were taken in mid-July on true color film (Kodak SO 397) to sample a larger area totaling 494,080 acres (McGregor and others 1972). Twenty-four plots were sampled by ground crews to obtain factors with which to correct photo interpretations of damage.

1973

In late July, 287,000 acres were surveyed by 186, 100-acre photo plots using color Ektachrome MS Aerographic 2448 Estar Base film. Thirty, 100-acre plots were selected for ground cruising to correct aerial photo interpretations and estimate damage (McGregor and others 1974). Faded trees were counted on each 100-acre photo plot, and a dot-grid was used to determine areas of merchantable forest as opposed to other areas. This stratification eliminated from the survey nonhost types as well as nonsusceptible younger age classes, such as pole stands and nonstocked areas.

1974

Because of decline of the outbreak and other commitments, aerial photography and ground surveys were discontinued. Instead, faded (1973-attacked) groups were observed and mapped from aircraft during August 12-13. Trees that were infested in 1974 were sought on the ground in August when sampling began. Such trees were scarce and difficult to identify so soon after being infested.

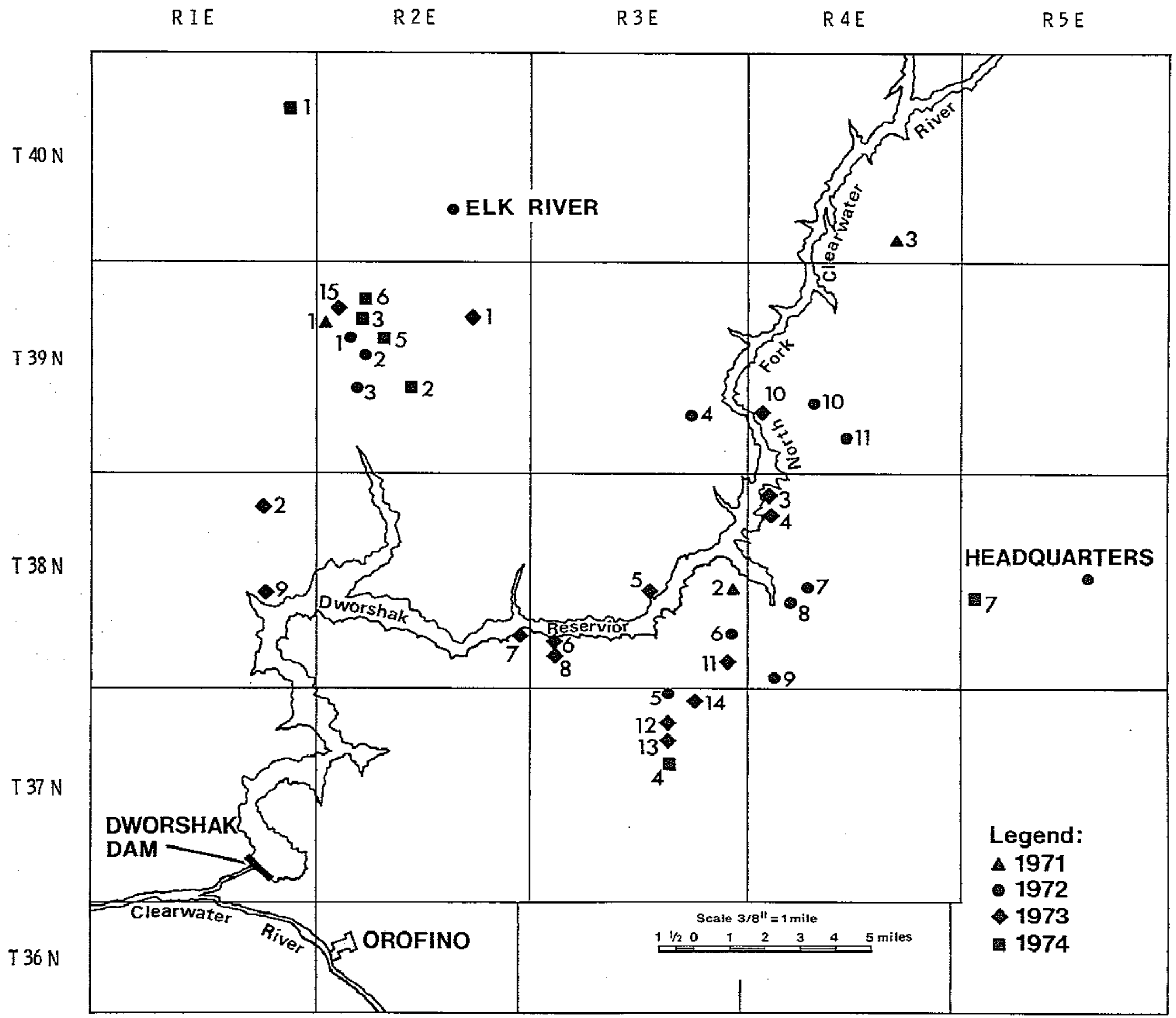

Figure 1.--Study area and location of sample groups of infested trees.

Population and Other Factors

THIRD GENERATION OF OUTBREAK (1971)

During October 27-November 1, 1971, we examined three infested groups of trees. All trees (468 total) in these groups were rated for success of beetle attack, and their diameters at breast height (d.b.h.) were measured. The percentage of trees attacked unsuccessfully (fig. 2A) was computed to indicate the importance of tree resistance in the eventual decline of the infestation.

Then, from each group 20 successfully attacked trees--trees in which the brood survived at least to larval stage--fig. 2B) were selected randomly from among all diameter classes. From each of these trees, two bark samples (1/10 ft^2 each) were removed from a height of ca 12 ft above ground (fig. 3A,B). The sampling punch and the distribution of Douglas-fir beetle attacks in standing trees have been described (Furniss 1962a,b). An 8-foot ladder was necessary to reach 10 ft or higher, where attacks are more uniform and representative of infestation in the tree.

A B

Figure 2.--A. Beetle galleries in a tree that survived attack. Such galleries produced no live brood. B. Successful galleries and larval mines in a killed tree.

Figure 3.--A. Population trend and abundance of predators and parasites were determined from bark samples taken with a circular punch 10 to 12 ft above ground. B. Bark sample containing Douglas-fir beetle egg galleries and larval mines.

A

B

We counted numbers of gallery starts (attacks), Douglas-fir beetle brood by stages, and immature parasites and predators by species. A Douglas-fir beetle population trend index (ratio of brood to attacking parents) was computed to relate to damage trend. Sample trees were then divided into categories of population trend. Those having a ratio of brood/parents >1 were designated "population generators" and those <1 were designated "population sinks."

FOURTH GENERATION OF OUTBREAK (1972)

Because we thought that the three large groups sampled in 1971 might be biased in size and too few in number, we sought a more representative sample in 1972. But infested trees were still green in appearance and difficult to find. To improve our search technique we tried the following procedures.

We sought to determine the closest distance between faded groups that appeared on aerial photo pairs taken in 1971 and 1972 (fig. 4). That is, we looked for a group that appeared on both years' photos; and another group that appeared only on the later photo of each pair. We intended to begin searching for 1972-infested trees (most were still green) at a radius of the minimum distance between groups of previous years. However, only five photo pairs covered the same ground area both years, and none had more than one year's group on it. Thus, beetles were shown to have flown from the group of their origin to distances beyond the scope of the photos. We think that this method might have worked earlier in the outbreak when infested groups were more abundant and therefore closer together.

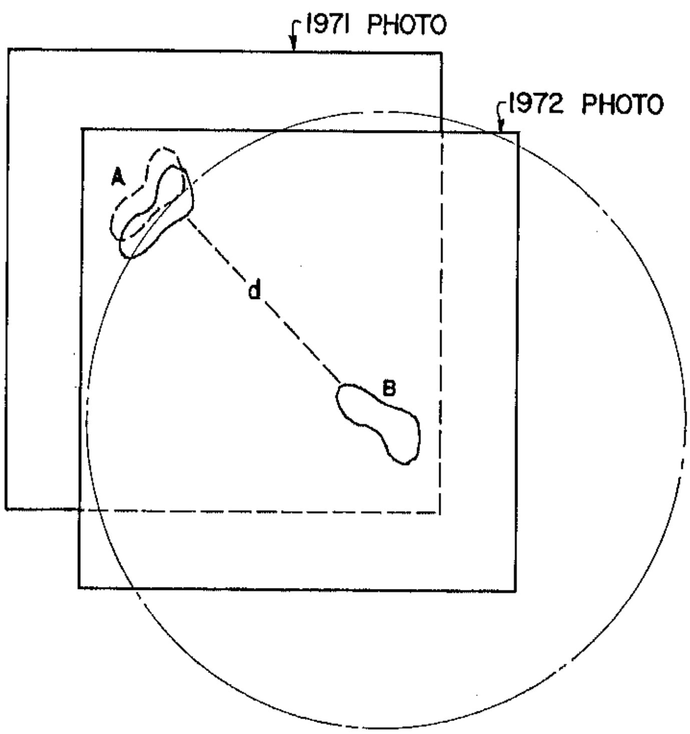

Figure 4.--Conceptual illustration of attempted method of sampling 1972-attacked trees. A is the same group visible on photos taken in 1971 and 1972. B is a group visible only on 1972 photos. Distance "d" between groups is the radius of search for 1972-attacked trees (still green) for comparative sampling.

Eventually, 11 groups were located after much searching and were sampled during September 5-October 6, 1972. Procedures during this sampling were similar to those in 1971, except that additional data were obtained including (1) physiographic features (elevation, aspect, and topographic position) and (2) presence of vegetation indicative of moistness and dryness. Moist sites were identified by grand fir; dry sites by grass or snowberry; and intermediate moisture conditions by ninebark or oceanspray (Daubenmire and Daubenmire 1968).

We also examined four groups (two 1971- and two 1972-attacked) and inventoried all trees greater than 7.6 inches d.b.h. within the perimeter of each group. From this inventory we calculated the proportion of Douglas-fir, the density of stems, and the basal area per acre. Because no local Douglas-fir stocking or yield table was available, we used yield tables for second-growth western white pine (Haig 1932), which occurred in parts of the study area. We referred to Deitschman and Green (1965) to relate heights of dominant Douglas-firs to white pine site index, from which we determined normal stocking. Site index was determined by measuring height and age of about 10 trees per group (Brickell 1968). Habitat type (Daubenmire and Daubenmire 1968) and soil depth were also determined.

We also tallied understory trees (less than 7.6 inches d.b.h.), by species, on ten 4-milacre quadrats per group. The quadrats were located randomly along lines at 50-ft intervals across the length of each group.

We checked the accuracy of previous ground estimates of success of attacks by examining beetle galleries higher in the trees with the aid of a ladder. Root rots were evaluated by falling six trees in two of the groups. These trees were chosen to represent extremes of beetle infestation and included both successfully attacked and unsuccessfully attacked trees. Then the soil around the roots was excavated by blasting (fig. 5). Kinds of rots were determined symptomatically by examining the exposed roots.

FIFTH AND SIXTH GENERATIONS OF OUTBREAK

In 1973, we located 15 groups of infested trees while they still appeared to be normal. However, because of a decline in the outbreak, we located only seven currently infested groups in 1974. All groups were inventoried and sampled by procedures used previously.

Figure 5.--Preparation for blasting to excavate dirt from roots to enable diagnosis of root rot infection.

RESULTS AND DISCUSSION

Damage Measurement

Volume of Douglas-fir killed during 1971-1974 was approximately 111 million bd.ft. or about 15.3 percent of the merchantable Douglas-fir stand (McGregor and others 1974; Hamel and others 1975). The damage trend during those years is shown in figure 6.

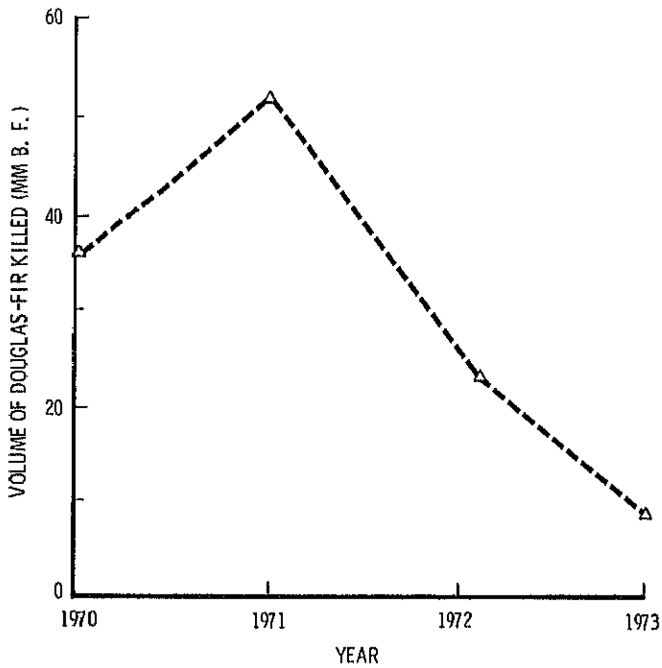

Figure 6.--Trend of Douglas-fir beetle infestation expressed in millions of board feet of Douglas-fir stand killed, 1970-1973.

Population and Other Factors

THIRD GENERATION OF OUTBREAK (1971)

Characteristics of attacked trees and groups.--The infested groups were large, averaging 158 trees (table 1). Such large groups were characteristic of those visible during the first two generations of the outbreak.[2] Average age of attacked trees was 97 years (R = 71-135). In the Rocky Mountains trees younger than 100 years seldom have been infested.

Examination of galleries disclosed that 31 percent of the trees appeared to have been attacked unsuccessfully. However, we re-examined two of these groups a year later and found that 14 percent of the trees originally classed as "unsuccessful" had, in fact, been killed (table 2). The error resulted from originally determining success of attack from the ground; while in checking accuracy, we used an 8-ft ladder to reach a height of 10 to 12 ft. Attacks were significantly more dense and successful above the height we could easily reach from the ground (Furniss 1962a). Later, a similar error (11 percent) was determined for two 1972-infested groups, so we think the 27 percent (58-31=27) increase in unsuccessful attacks between 1971 and 1972 (table 1) was not the result of errors in rating success of attack between the 2 years but was a real increase in resistance.

Table 1.--*Characteristics of sample groups of trees attacked by Douglas-fir beetles, 1971-1974*

Group	Age	Height	Number	Percent unsuccessful	D.b.h. unsuccessful	D.b.h. successful
		Feet			- - - - - - -*Inches*	- - - - - -
				1971		
1	106	--	113	26 (15)[1]	16.3 (15.7)	17.6 (17.5)
2	95	--	180 (187)	39 (22)	17.4 (14.8)	19.8 (20.0)
3	88	--	175	26	16.4	18.4
Average	97	--	158	31 (22)	16.7 (15.6)	18.7 (18.8)
				1972		
1	120	--	114	66 (53)	17.0 (17.3)	19.0 (19.0)
2	118	114	20	75	19.7	16.6
3	91	106	266	68	18.0	17.4
4	164	133	14	50	23.9	30.7
5	120	124	48	67	17.9	21.0
6	116	111	68	38 (29)	19.1 (20.9)	23.2 (23.0)
7	127	134	17	65	25.1	24.9
8	144	102	149	45	16.5	16.9
9	154	113	26	38	22.7	25.2
10	95	111	133	65	16.8	16.8
11	94	116	18	83	20.4	22.0
Average	118	116	79	58	18.0	19.1
				1973		
1	172	122	7	43	21.2	24.5
2	144	108	10	80	17.5	18.3
3	92	109	5	0	--	18.3
4	145	134	27	8	22.2	27.3
5	146	140	12	17	22.4	29.3
6	122	127	15	7	24.0	24.9
7	127	120	15	73	19.3	23.4
8	149	128	6	0	--	24.0
9	89	110	14	29	12.0	22.9
10	116	106	21	38	14.5	19.9
11	--	102	20	5	11.0	19.2
12	78	114	17	6	18.2	16.9
13	83	92	11	9	17.3	17.2
14	95	97	117	35	14.1	19.2
15	94	128	29	38	17.2	19.6
Average	117	113	22	29	16.0	21.1
				1974		
1	110	107	27	52	18.8	19.8
2	79	115	10	50	16.7	16.3
3	101	108	6	50	10.1	20.2
4	96	113	4	50	18.9	21.4
5	117	126	26	12	19.7	20.7
6	95	105	24	37	14.0	19.0
7	154	132	24	37	20.3	20.5
Average	110	116	17	35	17.4	19.9
4-year average	111	115	50	42	17.4	19.5

[1]Figures in parentheses were corrected later by examination using a ladder (see text).

Table 2.--*Accuracy of rating unsuccessfully attacked trees from ground and with ladder*

Group	Unsuccessfully attacked trees				
	Ground rated		Ladder rated		Difference
	No.	*Percent*	*No.*	*Percent*	*Percent*
1971-1	30	26	17	16	10
1971-2	71	39	41	23	16
1972-1	74	66	61	53	13
1972-6	29	38	20	29	9
Total	204		140		
Average		42		29	13

Within infested groups of rather uniform age, beetles killed larger (dominant) trees more frequently than smaller (suppressed) trees. Average diameter of killed trees was 18.6 inches; that of trees that survived attack was 15.6 inches. Larger, more dominant trees may be inherently more attractive to continued attack, leading to lethal attack densities. Smaller, suppressed trees although of equal age, may be less attractive, due to less resin exudation, resulting in sublethal attack density. For example, monoterpene vapors from resin stimulate pheromone production in several *Dendroctonus* beetles (Hughes 1973) and synergize the Douglas-fir beetle aggregating pheromone, frontalin (Furniss and Schmitz 1971). Dominant trees could still be more resistant than suppressed trees to a particular attack density, but the intense aggregation of large numbers of beetles on attractive dominant trees could result in more of them being killed than their more suppressed neighbors. We know from earlier work that the latter are attacked less densely.[3]

This tendency for beetles to kill larger trees in an unmanaged stand should not lead to the conclusion that larger trees would prove more susceptible in a managed stand. Just the opposite has been reported (Williamson and Price 1971). Shading of the stem may be an important factor. In thinned stands, more exposed stems would be less conducive to arrestment of beetles. For example, Douglas-fir beetles tend to concentrate their attacks on the shaded underside of sun-exposed windthrown trees (Furniss 1962a), probably due to their aversion of high temperatures (Vité and Rudinsky 1957).

Population trend.--Trend of beetle numbers during 1971 is shown in table 3. Samples with more progeny than parents (generators) made up 35 percent of the total. The remainder were static or were population sinks. Averaging the samples produced an overall population trend index of 1.1. That is, there were 10 percent more broods than parents that had attacked the samples. These broods consisted of new adults (86 percent), larvae (9 percent), and pupae (5 percent). The larvae would mature to adults in 1972, emerge, and attack weeks later than the overwintered adults. The broods would be subject to mortality from unknown factors during winter, during flight, and during invasion of new host trees. No one has accurately estimated the magnitude of such mortality in a Douglas-fir beetle generation. However, mortality does occur and we predicted (Ciesla and others 1971) that a final population index of 0.7 might prevail, arbitrarily assigning about 10 percent decrease to each of the above three categories. As it turned out, damage did diminish between 1971 and 1972 (fig. 6). Such a relationship between numbers of overwintered emerging adult beetles and numbers of trees infested subsequently has been recorded in New Mexico (Chansler 1968).

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[3]Unpublished data of senior author, presented at Second Forest Biology Workshop, Oreg. State Univ., Aug. 2, 1972.

Table 3.--*Population trend indices 1971-1974*

Group	Samples	Trend class and frequency: Generators	Static	Sinks	Population trend index
	Number	- - - - - - - - -	*Percent*	- - - - - - - -	*Average*
			1971		
1	42	41	18	41	1.4
2	40	35	0	65	1.1
3	40	30	20	50	0.8
Total	122				
Average		35	13	52	1.1
			1972		
1	20	30		70	0.8
2	10	40		60	1.0
3	20	60		40	1.2
4	14	57		43	1.1
5	20	30		70	0.8
6	20	40		60	1.3
7	12	50	17	33	1.0
8	20	30	20	50	1.0
9	20	50	10	40	1.4
10	20	50		50	1.0
11	6	67		33	1.3
Total	182				
Average		44	4	52	1.1
			1973		
1	8	0	25	75	0.0
2	4	0	50	50	0.0
3	10	20	0	80	0.6
4	20	20	30	50	0.9
5	20	40	10	50	1.5
6	20	60	0	40	1.5
7	8	75	0	25	3.2
8	12	33	0	67	0.8
9	20	60	0	40	1.0
10	20	20	0	80	0.5
11	20	10	0	90	0.2
12	20	30	0	70	0.6
13	20	40	0	60	0.5
14	20	40	0	60	1.3
15	20	20	10	70	0.4
Total	242				
Average		33	6	61	0.8
			1974		
1	20	50	0	50	1.2
2	10	50	25	25	2.0
3	6	100	0	0	5.0
4	4	100	0	0	--
5	20	70	0	30	2.9
6	20	80	10	10	3.2
7	20	70	10	20	2.1
Total	100				
Average		70	6	24	2.5

Natural enemies.--Abundance of larvae of predators and parasites on bark samples is shown in table 4. The braconid, *Coeloides brunneri* Vier., was most abundant followed by dolichopodids, *Medetera* spp. Clerids (*Thanasimus undatulus* Say and *Enoclerus sphegeus* [Fab.]) and the ostomid, *Temnochila chlorodia* (Mann.), were scarce. We know that *E. sphegeus* migrates to the root crown in midsummer, before we sampled. Why *T. chlorodia* was not more abundant is puzzling. Elsewhere *T. chlorodia* was relatively more abundant in an area where an infestation had subsided about two years previously. The relative abundance of certain predators such as *T. chlorodia* could be a key factor in evaluating outbreaks of the Douglas-fir beetle, but only further investigation will tell.

Table 4.--*Densities of natural enemies on bark samples, 1971-1974*

Group	Samples	*Coeloides brunneri*	*Medetera* spp.	Cleridae	*Temnochila chlorodia*
	Number	- - - - - - - - *Number per ft²* - - - - - - - -			
			1971		
1	42	12.6	0.7	0.2	0.2
2	40	6.2	0.7		
3	40	14.5	0.7	0.2	
Total	122				
Average		11.1	0.7	0.2	0.1
			1972		
1	20	14.5	0.5		
2	10	21.0	6.0		
3	20	28.0	1.0	1.0	
4	14	1.4	1.4		
5	20	10.5	0.5	0.5	
6	20	12.0		0.5	
7	12	9.1	1.7		
8	20	13.0	1.0		0.5
9	20	3.5	7.5	2.0	
10	20	19.0	1.5	0.5	
11	6	3.3	3.3		
Total	182				
Average		13.0	2.0	0.5	0.05
			1973		
1	8	--			
2	4	5.0			
3	10	4.0			
4	20	1.5			
5	20	--			
6	20	3.5	1.0		1.0
7	8	13.7	1.2		
8	12	10.0	0.8		0.8
9	20	7.5	3.5		2.0
10	20	2.5	1.0		
11	20	5.5	2.0		
12	20	5.5	0.5		
13	20	2.5	0.5		
14	20	16.0	1.5		
15	20	4.0	2.5		
Total	242				
Average		5.2	1.1		0.3
			1974		
1	20	16.5	2.5	0.5	
2	10	5.0	5.0		
3	6	6.7	5.0		
4	4	7.5	7.5		
5	20	8.5	3.0		
6	20	11.0	1.5		
7	20	10.0	0.5		
Total	100				
Average		10.4	2.6	0.1	

FOURTH GENERATION OF OUTBREAK (1972)

Characteristics of attacked trees.--The average age of attacked trees was 118 years (R = 72-186+) (table 1). Rate of successful attack increased with tree age and diameter.

Unsuccessfully attacked trees were proportionately more abundant in 1972 (59 percent) than in 1971 (31 percent). This may have been due to beetles having killed many of the more susceptible trees in 1972, and because weather was favorable to tree growth in 1972. Increased moisture is associated with increased resistance of trees to the Douglas-fir beetle (Rudinsky 1966). The host is a dominant factor in regulating Douglas-fir beetle populations; other biotic factors, such as predators, seem to be more limiting at lower population levels.

Characteristics of groups.--The size of groups varied considerably, ranging from 14 to 266 trees (table 1) but a general decline in group size was evident to aerial observers during 1972. Two of the larger groups (No. 1 and No. 3) resulted from attraction created by deployment of frontalin, an aggregating pheromone of the Douglas-fir beetle. We are not sure how representative they were.

The physiographic and stand characteristics related to groups are summarized in table 5. Within these groups, attacked Douglas-fir averaged 79 per acre. Elevations of sample groups ranged from 2,380 to 3,705 ft above sea level. Eight groups occurred on generally warm aspects, three groups on cooler aspects. Nearly all groups were located at midslope or higher and most were on upper slopes, due perhaps to Douglas-fir being more prevalent there and perhaps also to the beetle's flight behavior, and the rising of odors of trees and pheromones. Species of plants that indicate contrasting moisture conditions occurred in admixture and we conclude that a better measure of moisture availability is needed to seek to correlate that factor with susceptibility.

Two pairs of groups of attacked trees are compared in table 6. One member of each pair was attacked in 1971, the other in 1972. Group size ranged from ca 1 to 2 acres and average age varied from 95 to 120 years. Site indexes ranged from 77 to 83 (Brickell 1968), good for Douglas-fir growth. All were in the western redcedar-*Pachistima* habitat type, a further indication that the sites were productive. Soil was deep, with the exception of group No. 1 (1971) which had hardpan at 12 to 18 inches depth.

Infested stands ranged from 251 to 361 ft^2 basal area (81 to 124 percent of normal), substantiating our visual impression that they tended to be densely stocked (fig. 7). In three of the four groups we measured, Douglas-fir comprised 64 to 75 percent of the stand basal area; the fourth group was 49 percent Douglas-fir. Even the least of these percentages is relatively high for the mixed conifer stands commonly occurring in the cedar-*Pachistima* habitat type.

Results of sampling of understory trees less than 7.6 inches d.b.h. on ten 4-milacre quadrats per plot are summarized in table 7. The understory trees were 95 percent grand fir; the remainder were western redcedar. Understory trees may have added to moisture stress of Douglas-fir but will probably be more important in changing composition of the stand when released by killing of the overstory.

Population trend.--Trend of the beetle population during 1972 is contained in table 4. Although 52 percent of the samples were generators of brood, compared to 35 percent in 1971, the average trend index was 1.1 both years. However, the absolute population would have declined in proportion to the fewer number of successfully attacked trees in 1971 compared to 1972. As we have noted, the proportion of unsuccessfully attacked trees increased, and group size decreased during this period. The absolute population must, therefore, have decreased from 1971 to 1972.

Table 5.--*Physiographic features and moisture indices of groups of Douglas-fir beetle attacked trees, 1972-1973*

Group	Elevation	Aspect[1]	Slope position	Moisture index[2]
	Feet			
			1972	
1	2,700	SSE w	Midslope	1, 3
2	2,840	NNW c	Upper slope	1, 3
3	2,700	WSW w	Bench	1, 2, 3
4	3,070	WNW w	Upper slope	1, 2, 3
5	3,425	ENE c	Upper slope	1, 2, 3
6	3,290	SSW w	Ridge	1, 3
7	2,760	SSW w	Bench	3
8	2,380	WSW w	Ravine	1
9	3,700	SSE w	Ridge	1, 3
10	3,100	NW c	Midslope	1, 2, 3
11	2,920	WSW w	Midslope	1, 2, 3
			1973	
1	2,990	SSW	Ridge	1, 2, 3
2	3,005	S	Slope	3
3	1,710	SSE	Slope	1, 2
4	1,940	NW	Ridge	1, 2, 3
5	1,930	SSW	Slope	1, 2, 3
6	1,905	SSE	Slope	1, 2
7	1,710	NNW	Slope	1, 2, 3
8	1,730	NNW	Slope	1, 2, 3
9	1,650	ENE	Slope	1, 2, 3
10	1,700	W	Slope	1, 2, 3
11	3,650	SSE	Ridge	2, 3
12	3,380	SSW	Slope	1, 3
13	3,380	SSE	Slope	1, 3
14	3,670	SSE	Ridge	1, 2, 3
15	2,700	W	Slope	1, 2, 3
			1974	
1	3,675	N	Ridge	1, 2, 3
2	2,820	SSW	Slope	1, 2, 3
3	2,900	WSW	Slope	1, 2, 3
4	3,040	SSW	Ridge	1, 2, 3
5	2,950	NNW	Slope	1, 2, 3
6	3,100	WSW	Slope	1, 2, 3
7	3,500	NW	Slope	1, 3

[1]w = warm, c = cool aspect.
[2]Vegetation present: 1 = grass, snowberry (dry); 2 = ninebark, oceanspray (intermediate); 3 = grand fir (moist).

Table 6.--*Initial and residual stand density of groups killed by Douglas-fir beetle in 1971 and 1972*

Group		Stand age	Site index	Area	Trees per acre: Total	Trees per acre: DF	Trees per acre: % DF	Basal area per acre: Total	Basal area per acre: DF	Basal area per acre: % DF	Percent normal
Year	*No.*			*Acre*	*No./acre*	*No./acre*		*Ft²/acre*	*Ft²/acre*		
					Initial Stand[1]						
1971	1	106	82	1.26	240	152	63	278	202	73	96
1972	1	120	83	1.92	155	94	60	251	160	64	81
1971	2	95	80	2.16	220	143	65	340	233	68	124
1972	6	116	77	1.64	213	71	33	361	175	49	118
					Residual Stand[2]						
1971	1	106	82	1.26	149	62	41	133	57	43	46
1972	1	120	83	1.92	88	27	31	126	35	28	41
1971	2	95	80	2.16	133	56	42	159	52	33	58
1972	6	116	77	1.64	162	20	12	216	31	14	71

All groups are in cedar-*Pachistima* habitat type.

[1]Total stand includes the Douglas-fir trees infested with beetles.
[2]Residual stand remaining after infested Douglas-fir trees were subtracted.

Of the brood on the bark samples, 21 percent were immature (larvae 17 percent; pupae 4 percent), compared to 14 percent (larvae 9 percent; pupae 5 percent) in 1971. A shift toward immature overwintering brood has important implications. Instances have been recorded (Furniss 1965, McMullen 1970) in which infestations subsided when all brood eventually overwintered as larvae and stayed in the trees for 2 years. This was accompanied by high mortality of brood; but, exceptionally cold weather persisted prior to those events.

Figure 7.--A young stand attacked by Douglas-fir beetles. Overstocking and high proportion of Douglas-fir are factors involved when young stands are attacked.

Table 7.--*Stocking of understory trees in four groups attacked by Douglas-fir beetles in 1971 and 1972*

	Plot			
	1971-1	1971-2	1972-1	1972-6
Stocked quadrats (percent)	40	70	100	80
Trees (Σ No./acre)	200	450	1,200	875

Progressive increase in the proportion of immature brood overwintering may benefit a species. Weather and host conditions may alternately favor either early- or late-emerging brood (Atkins and McMullen 1958) due to seasonal change in precipitation and temperature. Such a possibility and lack of control over it makes prediction difficult. Additional documented case histories, such as ours, should assist in determining the probabilities involved.

Natural enemies.--Abundance of natural enemies of Douglas-fir beetles on bark samples during 1972 is shown in table 4. Their relative abundance was the same as during 1971. However, except for *C. brunneri*, they were less numerous per square foot in 1972, although a decline in number of trees killed should have resulted in their being more abundant per unit area of bark even if their populations remained static.

Root rot association.--All three trees that we examined in the first group for root diseases had been attacked by Douglas-fir beetles in the previous year. They had been rated as resistant, semiresistant and susceptible, based on success of beetle attack. Their roots contained galls below ground, which apparently developed after a fire more than 50 years ago. The galls varied in size and in extent of roots infected. In location and form, galls were similar to *Agrobacterium tumefaciens* (E.F. Sm. and Town.) Conn, but presence of other organisms precluded isolating the specific cause.

We also found *Armillaria mellea* (Vahl ex Fr.) Quél. associated with diseased roots of the three trees. In one root we found a spindle-shaped canker 100 cm x 8.5 cm with blue-black streaks beneath. In laboratory cultures, this canker yielded *Verticicladiella wagenerii* Kendr., the cause of "root-stain disease" (Leaphart 1960). This fungus was not known previously to infect Douglas-fir.

Two of the three trees that we selected from the second group had been attacked by beetles; one successfully and one unsuccessfully; the third tree had not been infested. We found extensive *A. mellea* in both beetle-attacked trees and *A. mellea* together with *Poria subacida* (Fr.) Sacc. and streaks suggesting root-stain disease in the unsuccessfully attacked tree. Cultures confirmed that *V. wagenerii* was associated with the streaks. All roots of the unattacked tree were healthy although it was surrounded by infested and infected trees.

The amount of root disease was generally correlated with success of beetle attack. Three trees with roots 70 to 90 percent destroyed were successfully invaded by beetles. Two with 30 to 40 percent root destruction had mostly unsuccessful attacks and one with no diseased roots had no attacks.

FIFTH GENERATION OF OUTBREAK (1973)

Characteristics of attacked trees.--Average age of attacked trees was 117 years (R = 80-183) (table 1).

Characteristics of groups.--Group size declined from an average of 79 to 22 trees between 1972 and 1973 (table 1) in spite of a record drought that summer. Proportion of unsuccessfully attacked trees also diminished, no doubt as a result of moisture stress (Rudinsky 1966).

Sample groups occurred between 1,650 ft and 3,670 ft elevation, mainly on warm slopes (table 5). Moisture indicating plants were again too diverse to be of utility in characterizing sites.

Population trend.--Trend of beetle population declined to a ratio of 0.8 brood per parent (table 3) and less than 1 percent of the overwintering brood was immature compared to 21 percent in 1972 and 14 percent in 1971. The faster rate of maturation was doubtless due to the warmer weather in 1973, a year of record drought.

Natural enemies.--*C. brunneri* continued most abundant among natural enemies followed by *Medetera* spp. (table 4). However, density of most natural enemies declined from the previous year, perhaps influenced by the decline in average productivity of Douglas-fir broods (table 3).

SIXTH GENERATION OF OUTBREAK (1974)

Characteristics of attacked trees and groups.--Average age of attacked trees was 110 years (R = 79-154) (table 1). Thirty-seven percent of the attacked trees were rated unsuccessful, up 8 percent over 1973.

Average number of attacked trees per group was 17, lowest of the 4 years. Infested groups occurred on ridges and drier slopes, from 2,790 to 3,650 ft above sea level (table 5). Groups occurred predominantly on warm aspects, but not necessarily at frequency different from green Douglas-fir, which predominates on warm aspects.

Population trend.--Population trend index (2.5) increased threefold over 1973 (table 3). Reasons for the increased population may be due to the 1973 drought which resulted in high moisture stress in trees, effects of which may have persisted in 1974 (Rudinsky 1966). Also involved in the higher population may have been a lower attack density ($6.9/ft^2$) in 1974 compared to $9.5/ft^2$ in 1973, which would have resulted in less intraspecific competition and consequent greater brood survival (Schmitz and Rudinsky 1968; McMullen and Atkins 1961). The high population index resulted in a threefold increase in damage in the Clearwater River drainage when the broods emerged in 1975 (Livingston and others 1977).

Natural enemies.--The larval parasite, *Coeloides brunneri*, continued to be the most prevalent natural enemy followed by *Medetera* spp. (table 4). The ostomid, *Temnochila chlorodia*, was absent from samples and only one larva of the clerid, *E. sphegeus* was tallied.

CONCLUSIONS

We note the following, based on our observations of the infestation: (1) Attacked groups were on good sites typical of the Clearwater drainages--in stands composed mainly of Douglas-fir, and that were denser than normal. (2) Age of attacked groups varied; but some averaged only ca 90 years old, unusually young in relation to other Rocky Mountain infestations. (3) Rate of tree-killing declined in the fourth beetle generation (1972). (4) The decline in the infestation was accompanied by cessation of major stand disturbances, smaller groups of infested trees, higher proportion of unsuccessfully attacked trees, and an average beetle population index of 1.1 in early fall. (5) Little change was apparent in density of immature parasites and predators on bark samples between years, and several were scarce on samples throughout our study. (6) Tree susceptibility to beetle attack may be related to infection by root rots.

Additional outbreaks should be studied similarly, for a longer period, especially at their inception, but factors that seem related to the onset or decline of an outbreak are: disturbances, stand density, success of attack (host resistance), population index, root rot, and, possibly, habitat type. All warrant further study.

We offer the following verbal model to describe the functioning of factors that regulate Douglas-fir beetle abundance and damage in the Northern Rocky Mountains:

> Disturbances such as windstorms and fire contribute to increased Douglas-fir beetle populations. When such disturbances cease, beetles seek out and attack live trees; their success depends upon the susceptibility of the attacked trees. Trees damaged by snow-breakage, possibly those defoliated by tussock moths, stressed by drought, or infected with root rots are susceptible and contribute to furtherance of the outbreak.
>
> The proportion of Douglas-fir in a stand, and its density and age are positively correlated with susceptibility. Any of these factors can limit damage, but high density can result in somewhat younger trees being attacked.

As the susceptible trees are killed by beetles or removed by logging, or, as the environmental conditions improve (favoring growth and water relations), resistance to population expansion mounts. Size of infested groups declines and a higher proportion of attacked trees survive. Numbers of natural enemies appear to be independent of prey density; influence of enemies increases after the bark beetle population subsides. Populations are maintained at an endemic level primarily by tree resistance and natural enemies.

We recommend that managers seek to prevent outbreaks by: (1) thinning young stands and maintaining desirable spacing until harvest, and (2) removing susceptible trees such as those that are windthrown, snow-broken, or infected with root rot. Such preventive action is the most effective and economical method for combatting beetle damage.

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1979. Chronology and characteristics of a Douglas-fir beetle outbreak in northern Idaho. USDA For. Serv. Gen. Tech. Rep. INT-59, 19 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Occurrence of the outbreak was associated with felled and damaged trees, dense stands of Douglas-fir, predominantly on good sites, and possibly root rots. Tree mortality began declining during the third year of the infestation, accompanied by increased resistance of trees to attack; a beetle population index of 1.1 in the fall, and a higher proportion of immature overwintering brood. A verbal model is proposed to describe the functioning of factors that regulate beetle populations and damage. Preventive measures are suggested.

KEYWORDS: Douglas-fir beetle, population dynamics, natural control, sampling, damage.

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BACK COVER:
Vertical view of Dworshak Reservoir with log debris from clearing. Douglas-fir beetle killed trees are visible in lower left.